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# Impacts of suburbanization on food web stoichiometry of detritus-based streams

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# IMPACTS OF SUBURBANIZATION ON FOOD WEB STOICHIOMETRY OF DETRITUS-BASED STREAMS

BY

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# ABSTRACT

IMPACTS OF SUBURBANIZATION ON FOOD WEB STOICHIOMETRY OF DETRITUS-BASED STREAMS

by

Nathaniel B. Morse

University of New Hampshire, December, 2010

Higher non-point source nutrient inputs are one of many impacts associated with the "urban stream syndrome". Research on how non-point source pollution affects the stoichiometry of urban stream food webs has received little attention, however. This study quantified food web stoichiometry in nine headwater, detritus-based streams draining forested or suburban watersheds in northeastern, coastal Massachusetts.

Suburban nutrient enrichment changed the nutrient quality of basal food resources. The nutrient content of most macroinvertebrate taxa did not change; however, some taxa did exhibit deviation from strict homeostasis. Combined, these changes have the potential to affect food web dynamics in suburban streams, and to shorten nutrient uptake lengths and increase nutrient recycling rates by consumers.

While this study suggests that suburbanization can affect in-stream nutrient recycling by consumers, research that quantifies changes to biomass of different in-stream compartments is needed to calculate the extent of such impacts on suburban stream ecosystems.

# INTRODUCTION

Land-use change is one of the greatest drivers affecting global ecosystems (Grimm *et al.*, 2008a). The conversion of rural and natural areas to urban and suburban systems modifies the structure, function and dynamics of local ecosystems (Paul and Meyer, 2001, Walsh *et al.*, 2005, Grimm *et al.*, 2008b). Impacts to stream ecosystems include physical changes in geomorphology , flashier hydrology, disruptions to water chemistry, and changes to stream biota, collectively known as the "urban stream syndrome" (Paul and Meyer, 2001, Walsh *et al.*, 2005). This urban stream syndrome affects both community structure and ecosystem function, with resulting impacts on downstream ecosystems (Meyer, Paul and Taulbee, 2005).

One symptom of the urban stream syndrome are increases in nutrient inputs (Paul and Meyer, 2001, Meyer *et al.*, 2005, Walsh *et al.*, 2005). Urban and suburban watersheds are not only associated with point and non-point sources to the landscape (Malmquist and Rundle, 2002), but also with decreased efficiency in removing and retaining nitrogen (N) and phosphorus (P), resulting in higher nutrient inputs to streams (Wollheim *et al.*, 2005, Withers and Jarvie, 2008). Point source pollution in the United States has declined significantly since the implementation of the Clean Water Act in 1972, leaving non-point source pollution as the most important current source of lake, stream and coastal eutrophication (Carpenter *et al.*, 1998). Greater non-point source pollution in urban and suburban watersheds is driven by a combination of high impervious area and more nutrient sources (e.g. fertilizers and human waste), with headwater streams being particularly vulnerable to increased nutrient inputs (Withers and Jarvie, 2008).

One way to assess the effects of shifting nutrient inputs into an ecosystem is to use the concepts of ecological stoichiometry. Ecological stoichiometry considers the flow and transfer of key elements through ecological interactions (Reiners, 1986, Sterner and Elser, 2002). Evaluating the chemical composition (nutrient content and relative nutrient ratios) of ecosystem components provides information on physiological, behavioral, and environmental stresses on organisms in an ecosystem (Sterner and Elser, 2002, Cross *et al.*, 2005). The concepts of ecological stoichiometry can also be used to understand better the feedbacks that mediate how consumers affect their environment (Sterner, Elser and Hessen, 1992, Elser *et al.*, 1998, Vanni, 2002). By evaluating the nutrient content of food resources, consumers, and the nutrient imbalance between the two, ecologists can make predictions about how consumers affect nutrient cycling within the ecosystem (i.e. consumer-driven nutrient cycling (Vanni, 2002).

Stoichiometric homeostasis, defined as the maintenance of an organism's nutrient content within a narrowly defined range relative to that of its food resources, is important to consider in such analyses (Sterner and Elser, 2002). If a consumer is not homeostatic, then changes to nutrient inputs into an ecosystem could change the consumer-driven nutrient recycling rates, which could subsequently affect overall nutrient cycling (Small, Helton and Kazanci, 2009). If an organism is homeostatic, then consumers would have little impact on changes to nutrient cycling in the system. While many food resources respond to changes in nutrients by shifting their elemental content, it was originally thought that consumers underwent only minor variations in nutrient content (Sterner and Elser, 2002). However, recent research has demonstrated that some macroinvertebrate

species show variable elemental content, especially in P, due perhaps to storage of excess nutrient (Cross *et al.*, 2003, Cross *et al.*, 2005, Frost *et al.*, 2005).

Alterations in nutrient imbalances between consumers and their respective food source also affect food web structure and function. In an experimental study, addition of N and P to a North Carolina forest stream shifted the elemental stoichiometry of some macroinvertebrate taxa (Cross *et al.*, 2003). Effluent from a sewage treatment plant in the Canadian Rockies affected stoichiometry of basal food resources; both C:P and C:N were lower downstream of the effluent discharge than upstream. Consequently, invertebrate community composition was different and total biomass was also higher (Bowman, Chambers and Schindler, 2005). Phosphorus enrichment from a wastewater treatment plant in Austria led to a shift in macroinvertebrate community structure towards faster-growing P-rich consumers, including a shift in C:N of some consumer taxa, indicating a lack of homeostasis for certain species (Singer and Battin, 2007). .

Although research on stoichiometric changes to nutrient-enriched stream ecosystems has focused on point source inputs, non-point source pollution is a greater source of nutrients than point sources(Carpenter *et al.*, 1998). The main objective of this project was to quantify the stoichiometric consequences of non-point source nutrient pollution for headwater, detritus-based streams draining suburban areas. Nine different streams, representing three classes of nutrient enrichment, were sampled to quantify the stoichiometry of their food web components and the imbalances between food resources and consumers. We hypothesized that higher in-stream nutrient loads in suburban streams would cause higher nutrient content of basal food resources. Furthermore, we predicted that higher N and P loads for streams within suburbanized watersheds would

yield lower nutrient imbalances between basal food resources and macroinvertebrates. Finally, we predicted that increases in nutrient content of basal food resources would be propagated up the food chain, resulting in higher P content of some macroinvertebrates. These combined stoichiometric responses to non-point source pollution should potentially affect nutrient cycling in suburban streams, with subsequent impacts on downstream aquatic ecosystems.

# CHAPTER I: METHODS

## Study Sites

Food web samples, including basal food resources and benthic macroinvertebrates, were collected during the spring and summer of 2008 from nine headwater stream reaches with diverse dissolved N:P ratios caused by different degrees of suburbanization in the watersheds. All sampling sites were located in the Parker and Ipswich River basins located in northeastern Massachusetts, USA. Both rivers drain low to moderate relief coastal lowlands, and their watersheds in general have relatively poor drainage (Baker, Healy and Hackett, 1964). Rainfall averages 1150 mm/yr, with little variation in seasonal precipitation (Claessens *et al.*, 2006).

Streams were selected to fit in one of three stream groups. Reference (REF) streams had low TDN and $PO_4^{3-}$ concentrations and watersheds with little urban development. The remaining six streams were selected from more urbanized watersheds, representing a range of suburban development. Of these, three had high TDN loads, but lower $PO_4^{3-}$ concentrations (N streams), and three had high TDN and $PO_4^{3-}$ concentrations (N+P streams; Table 1). The nine streams were chosen for sampling based on similarities in physical structure and riparian coverage. All stream reaches were wadeable during baseflow, of moderate gradient, and had gravel/cobble substrate and dense, deciduous riparian zones that severely limited in-stream autotrophic production during the growing season. Further selection was accomplished by opting for streams with specific nutrient loads using stream nutrient data collected as part of an earlier study

(Wollheim *et al.* (2005). Each stream was sampled three times during the growing season to characterize the stoichiometry of leaf litter, fine benthic organic matter (FBOM), epilithon, and benthic macroinvertebrates. These intensive sampling events were designed to sample each component in the headwater stream food web. In addition, monthly water and suspended particulate organic matter (SPOM) samples were collected to confirm nutrient status (see below).

**Table 1.** Watershed characteristics for the nine study streams in coastal Massachusetts, USA.

| Stream Group | Stream Name | % Impervious | Population Density (persons/km$^2$)* | Watershed Area (km$^2$)* |
|---|---|---|---|---|
| N+P | IS_103 | 26.4 | 1149.2 | 0.6 |
| | IS_169 | 11.5 | 174.8 | 0.6 |
| | IS_122 | 6.0 | 309.3 | 1.4 |
| N | IS_102 | 25.2 | 979.2 | 3.8 |
| | IS_152 | 11.7 | 418.7 | 1.5 |
| | IS_128 | 7.3 | 346.1 | 0.9 |
| Ref | PS_109 | 6.9 | 157.6 | 1.3 |
| | IS_140 | 4.0 | 124.1 | 1.5 |
| | CC | 8.2 | 130.4 | 3.8 |

* Population density and watershed area were calculated by Wollheim et al. 2005.

## Water Chemistry

Monthly water samples were collected from October 2007 through September 2008. These samples included both unfiltered samples and samples filtered using 0.7-µm pre-combusted Whatman GF/F filters. All filtered samples were analyzed for $NO_3^-$, $SO_4^-$, $Ca^{2+}$, $Cl^-$, $Mg^{2+}$, and $Na^+$ using a Dionex ICS-1000 Dual Channel Ion Chromatograph (Dionex Corp., Sunnyvale, CA). $NH_4^+$ and $PO_4^{3-}$ were measured using colorimetric methods on a Smartchem autoanalyzer (Westco Scientific Instruments, Brookfield, CT) on filtered stream samples. TN and TP were both measured by digesting the unfiltered stream samples using an alkaline digestion method (United States Geological Survey,

2003), followed by colorimetric analysis on the Smartchem. TDN was measured by digesting filtered stream samples. DON was estimated by subtracting $NO_3^-$ and $NH_4^+$ concentrations from TDN.

## Organic Matter

Suspended particulate organic matter (SPOM) was collected concurrently with monthly water samples. SPOM was collected by filtering stream water through a pre-weighed 0.7-µm GF/F filter. Epilithon was collected using a wire brush from cobbles and large gravel during macroinvertebrate sampling (see below). Fine benthic organic matter (FBOM) was sampled three times throughout the growing season. FBOM was collected from the stream bottom by agitating the top layer of collected organic matter and sampling the re-suspended organic matter. All samples were composites from 3 or 4 different locations throughout the sample reach. Ten natural, in-situ leaf litter samples were collected at random from each site during macroinvertebrate sampling. Additionally, five litter-bags (35 × 15 cm with 5-mm polypropylene mesh) containing 5 g (±0.1 g) of naturally senesced red maple (*Acer rubrum*) leaves were placed in each stream approximately two months before each intensive sampling event to quantify the influence of in-stream nutrient concentrations on leaf litter stoichiometry. After weighing and drying all litter samples, the natural litter packs were combined and homogenized with a Wiley Mill, while a separate sample from the litter-bags was homogenized.

Epilithon and FBOM samples were filtered in the lab using pre-weighed 0.7-µm GF/F filters. Both leaf litter samples and filters were dried for a minimum of 48 h at 60°C and weighed (±0.1 mg). All organic matter samples were analyzed for CNP content

using the same methodology. For C and N analysis, samples were analyzed using a Perkin Elmer (Waltham, MA) Series II CHNS/O Analyzer 2400. P content was quantified using an alkaline persulfate digestion followed by molybdate blue colorimetry. All data are presented as %C, %N, or %P of dry mass or as molar ratios.

## Macroinvertebrates

Macroinvertebrates were collected using the EPA Environmental Monitoring and Assessment Program for Surface Waters protocol (Baker, Peck and Sutton, 1997), with minor modifications. Large invertebrates were immediately separated and frozen; smaller invertebrates retained on stacked sieves (125- to 250-μm mesh size) were placed on ice and separated from benthic material using a dissecting scope within 12 h, before being frozen. All samples were identified to the lowest possible taxonomic level, measured (±1 mm), frozen, lyophilized, weighed, and homogenized to a fine powder using a spatula. Macroinvertebrates were analyzed for nutrient content as above. Functional feeding groups (FFG) were designated according to Merritt and Cummins (1996). These FFGs included scrapers (scrape biofilm from benthic surfaces), shredders (consume coarse particulate detritus), collector-gatherers (gather fine organic matter), collector-filterers (filter suspended organic matter) and predators (consume other animals).

## Statistical Analyses

All data were first tested for normality using the Shapiro-Wilk goodness-of-fit test. Data that did not meet criteria were either log or arcsine-square root transformed. To test for the effect of ambient nutrient regime on %P, %N, C:P, C:N, and N:P of stream

basal resources, macroinvertebrate order, FFG, taxa, and nutrient imbalances, we used analysis of variance (ANOVA) with stream group (REF, N and N+P) as the factor. We followed significant ANOVAs with Tukey's HSD multiple comparisons to test explicitly the influence of stream nutrients on specific groups (e.g. individual taxa). Coefficients of variation (CV) of nutrient contents and ratios of macroinvertebrates within stream groups were calculated to assess overall variation in stoichiometry within stream communities.

Stepwise multiple regression was used to determine the influence of stream nutrients on nutrient contents and ratios within each food web. Surface water total N, total P, TDN, $PO_4$, DOC, TN: TP, DOC:TDN, DOC: $PO_4$, and TDN: $PO_4$ were all included as potential independent variables to assess influence on stream food webs. Significant factors from the stepwise multiple regression were analyzed in individual linear regressions to explore patterns of significant influences on nutrient contents.

# CHAPTER II: RESULTS

## Dissolved Nutrient Concentrations

During the ten-month sample period, TDN was more than three times higher in urban streams (N and N+P) than in Reference (REF) streams (Table 2). $PO_4^{3-}$ concentrations were twice as high in the N+P streams than in the REF and N streams. Across all streams, TDN ranged from 5.6 to 149.2 μM and $PO_4^{3-}$ from 0.2 to 1.2 μM. The N:P ratios of the streams ranged from 28 to 449, with the REF and N+P streams having lower N:P ratios than the N streams (Table 2). There was no relationship ($r^2$=0.02, $P$=0.27) between in-stream TDN and $PO_4$ concentrations.

**Table 2.** Average nutrient concentration data for study streams from samples collected during the study period (Oct 2007 – Sept 2008). N:P is presented as a molar ratio.

| Stream Group | Stream Name | TDN (μM) | $PO_4^{3-}$ (μM) | N:P |
|---|---|---|---|---|
| N+P | IS_103 | 54.67 | 0.66 | 83 |
| | IS_169 | 49.44 | 1.20 | 41 |
| | IS_122 | 149.18 | 0.46 | 323 |
| N | IS_102 | 69.38 | 0.23 | 296 |
| | IS_152 | 97.51 | 0.24 | 400 |
| | IS_128 | 98.12 | 0.22 | 449 |
| Ref | PS_109 | 15.09 | 0.22 | 68 |
| | IS_140 | 5.63 | 0.20 | 28 |
| | CC | 13.72 | 0.27 | 52 |

## Basal Resources

N:P ratio of epilithon, FBOM and SPOM were lower in both the N and N+P compared to REF streams, whereas in-stream leaf litter only differed among the urban streams (Fig. 1). No differences or patterns were observed in the nutrient stoichiometry

of the litter bags (data not shown). Epilithon in the REF streams had higher N content than epilithon in the urban streams (Ref vs. N, $P$=0.0002; Ref vs. N+P, $P$=0.002) and N:P (Ref vs. N, $P$<0.0001; Ref vs. N+P, $P$=0.001). SPOM had the highest within-group variability of the basal resources and was the only basal resource with significant differences across stream categories for %C, %N and %P. N:P ratios of basal resources were most responsive to in-stream concentrations, with significant differences among stream groups for three of the four basal food resources (ANOVA $P$ values between 0.0001 and 0.047).

The multiple regressions also showed that leaf litter was less affected by stream nutrients than other basal food resources. Only the model for natural leaf litter %P yielded a significant result, compared to %P, %N, C:N, C:P and N:P for epilithon, FBOM and SPOM (Table 3). The models with the best fit were for epilithon %N ($r^2$=0.47), epilithon C:N ($r^2$=0.45), epilithon N:P ($r^2$=0.47), FBOM N:P ($r^2$=0.56), SPOM %N ($r^2$=0.44) and SPOM C:N ($r^2$=0.55). The independent variables most commonly included in the models of best fit were TDN, $PO_4$, TN:TP, and DOC:$PO_4$.

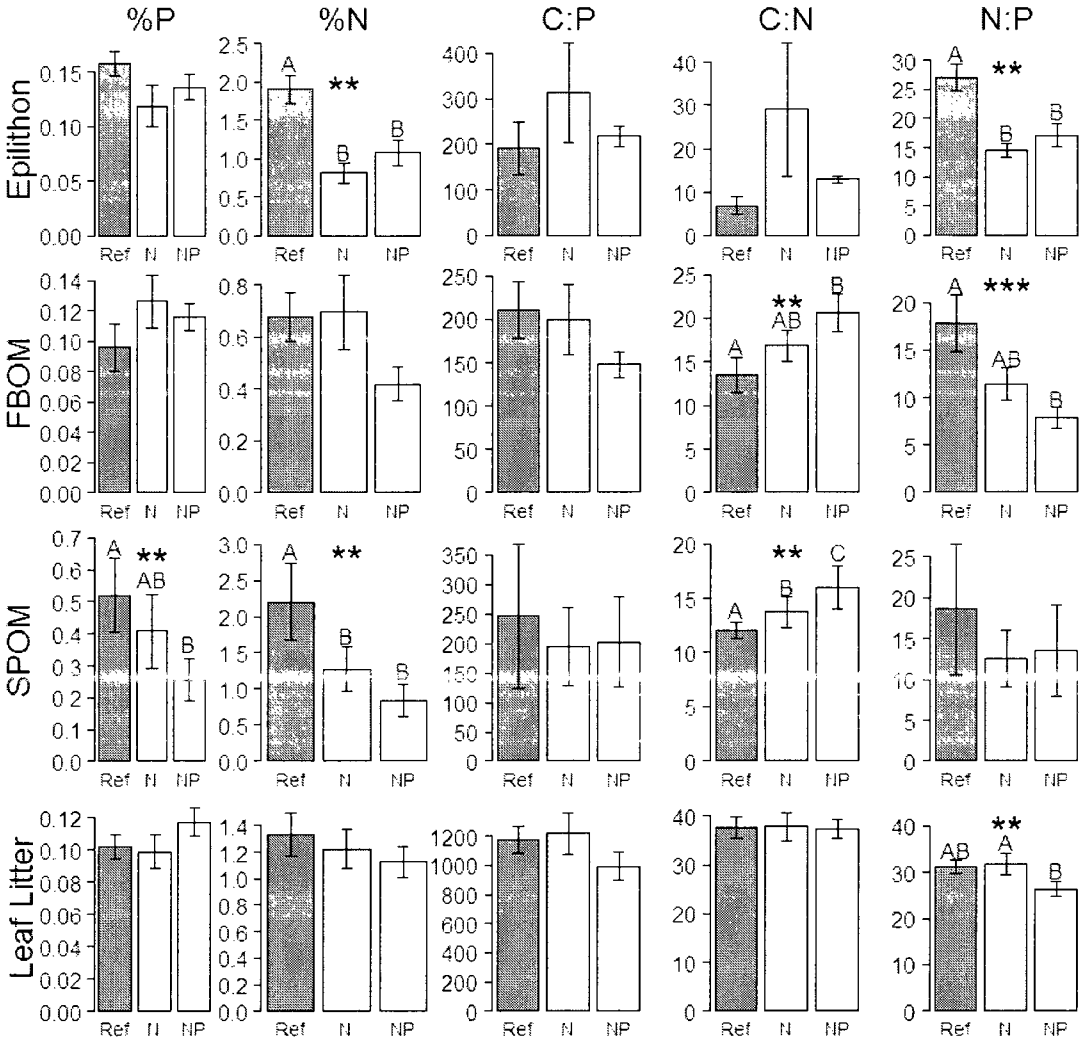


**Figure 1.** Mean nutrient content and ratios of the basal food resources sampled for each of the stream groups. Error bars ($n$=3) represent $\pm$1 SE. Different letters above the SE bars indicate significant differences between samples from the stream groups: **=$P$<0.05, ***=$P$<0.01.

**Table 3.** Multiple regression results for models with $r$-squared values greater than 0.1 and $P<0.05$. Dependent variables are stoichiometric variables for food web components, and independent variables are all stream nutrient characteristics.

| Dependent Variable | Significant Independent Variables | $r^2$ Value |
|---|---|---|
| Epilithon %P | TN:TP | 0.23 |
| Epilithon %N | $PO_4$, TN:TP | 0.47 |
| Epilithon C:N | $PO_4$, DOC, DOC:TDN | 0.45 |
| Epilithon C:P | DOC, DOC:$PO_4$ | 0.22 |
| Epilithon N:P | $PO_4$, TDN, $PO_4$ | 0.47 |
| FBOM %P | TP | 0.14 |
| FBOM %N | TDN, TN:TP, DOC:TDN | 0.36 |
| FBOM C:N | TN, TN:TP | 0.25 |
| FBOM C:P | DOC:TDN | 0.1 |
| FBOM N:P | TDN, TN:TP | 0.56 |
| SPOM %P | TN:TP, $PO_4$, DOC:$PO_4$ | 0.25 |
| SPOM %N | TDN, DOC:$PO_4$, $PO_4$, TN | 0.44 |
| SPOM C:N | TDN, $PO_4$, TN:TP, DOC:$PO_4$, TDN, $PO_4$ | 0.55 |
| SPOM C:P | TN:TP, $PO_4$, DOC, TDN | 0.26 |
| SPOM N:P | TN:TP, TDN | 0.3 |
| In-situ Leaf Litter %P | $PO_4$, TDN | 0.2 |

Basal food resource N:P declined as both N and P concentrations in stream water increased. Epilithon and FBOM N:P were negatively correlated with both TDN and $PO_4$, while SPOM was only correlated with TDN (Fig. 2). There was no significant relationship between in-stream leaf litter N:P and in-stream nutrient concentrations. The strongest relationship was between FBOM N:P and TDN ($r^2 = 0.44$).

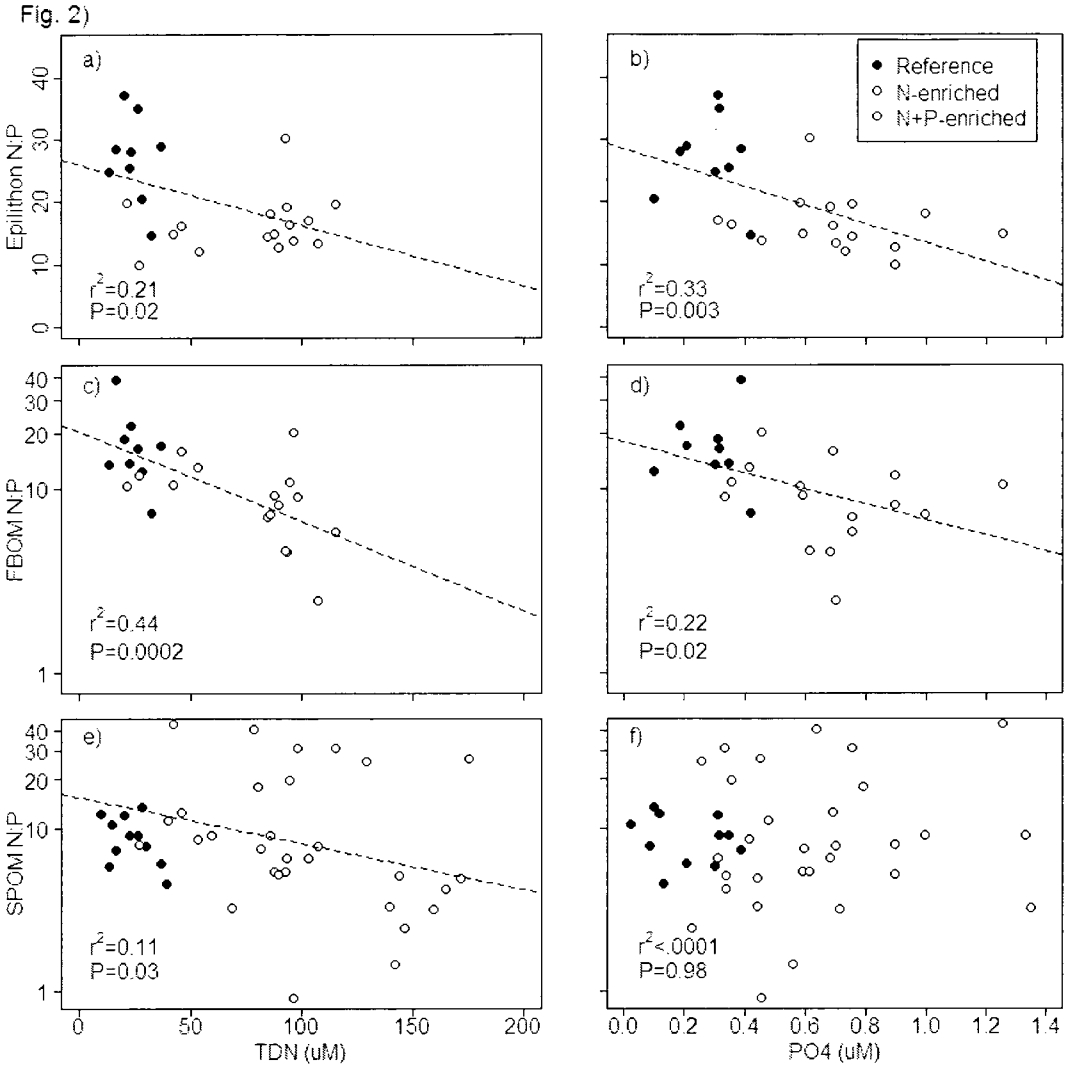


**Figure 2.** N:P ratios of epilithon, FBOM, and SPOM samples plotted against the TDN and $PO_4$ concentrations of the stream when samples were collected. Dashed lines represent the linear regression with $r^2$ and *P*-values in the lower left corner of each graph. FBOM and SPOM N:P are plotted on log scales.

## Macroinvertebrates

ANOVA results of the 565 macroinvertebrates sampled from all reaches demonstrated that order, FFG, and genus had a greater influence on body stoichiometry than did stream nutrient enrichment (Table 4). Higher suburban nutrient loads in the N+P streams did not affect the mean P content (0.9%) of the sampled macroinvertebrate

community, but they did lower the mean N content of macroinvertebrates in the N+P streams (7.6%) compared to the REF (8.5%) and N (8.2%) streams (REF vs. N+P, $P$=0.004; N vs. N+P, $P$=0.016).

**Table 4.** ANOVA results for nutrient content of all analyzed organisms. Independent variables are listed as column headings, and the dependent variables are defined as row headings. Significant differences are in bold.

| | n | Order | FFG | Genus | Stream Group |
|---|---|---|---|---|---|
| %P | 358 | **<0.0001** | **<0.0001** | **<0.0001** | 0.5203 |
| %C | 176 | **<0.0001** | **<0.0001** | **<0.0001** | 0.1667 |
| %N | 176 | **<0.0001** | **<0.0001** | **<0.0001** | **0.0008** |
| C:N | 176 | **<0.0001** | 0.3912 | **<0.0001** | 0.1097 |
| C:P | 131 | **<0.0001** | **0.0119** | **<0.0001** | 0.9220 |
| N:P | 131 | **<0.0001** | **0.0336** | **<0.0001** | 0.7517 |

Although the N-content of macroinvertebrates was the only factor with a significant response to nutrient enrichment, macroinvertebrate stoichiometry (both N- and P-content) was more variable within suburban than REF streams (Table 5). There was higher variation in %P (CV range: 29%-37%) among the macroinvertebrates than in %C (CV range: 15%-16%) or %N (CV range: 16%-20%). The highest variation in %P (CV=37%) and %N (CV=20%) were both in the streams with high N loads, while the reference streams had the lowest %P variation (CV=29%). Suburban streams with high N and high P loads had the lowest %N variation (CV=16%). Variation in C:P and N:P ratios of the macroinvertebrates followed the same trend as %P variation, with high-N streams having the highest variation and reference streams with the lowest variation. There was little difference between stream groups for %C and C:N.

**Table 5.** Coefficients of variation for elemental content variables measured in macroinvertebrate communities from each of the stream groups.

| | N | N+P | Ref |
|---|---|---|---|
| **%P** | 37% | 35% | 29% |
| **%C** | 15% | 15% | 16% |
| **%N** | 20% | 16% | 18% |
| **C:N** | 18% | 18% | 17% |
| **C:P** | 50% | 45% | 31% |
| **N:P** | 46% | 39% | 29% |

Stream group affected the stoichiometry within only some macroinvertebrate orders. Of the orders that did exhibit differences among stream groups, the patterns were inconsistent (Fig. 3). In all stream groups, Coleoptera had the lowest average P content. Amphipoda in N-enriched streams had significantly higher average N and P content than those in REF streams ($P<0.05$ for both N and P). In contrast, Diptera in REF streams had higher N and P content than Diptera in the other stream groups ($P\leq0.05$).

P content of functional feeding groups differed more than N content, but as with order, nutrient enrichment did not affect the stoichiometry of most FFGs. Scrapers had the lowest average P content among the FFGs, while none of the FFGs had substantially higher or lower N content (Fig. 4). The P content of predators in the N stream groups was higher than in the N+P streams ($P=0.03$). No other FFG had a significant difference in any measure of body stoichiometry.

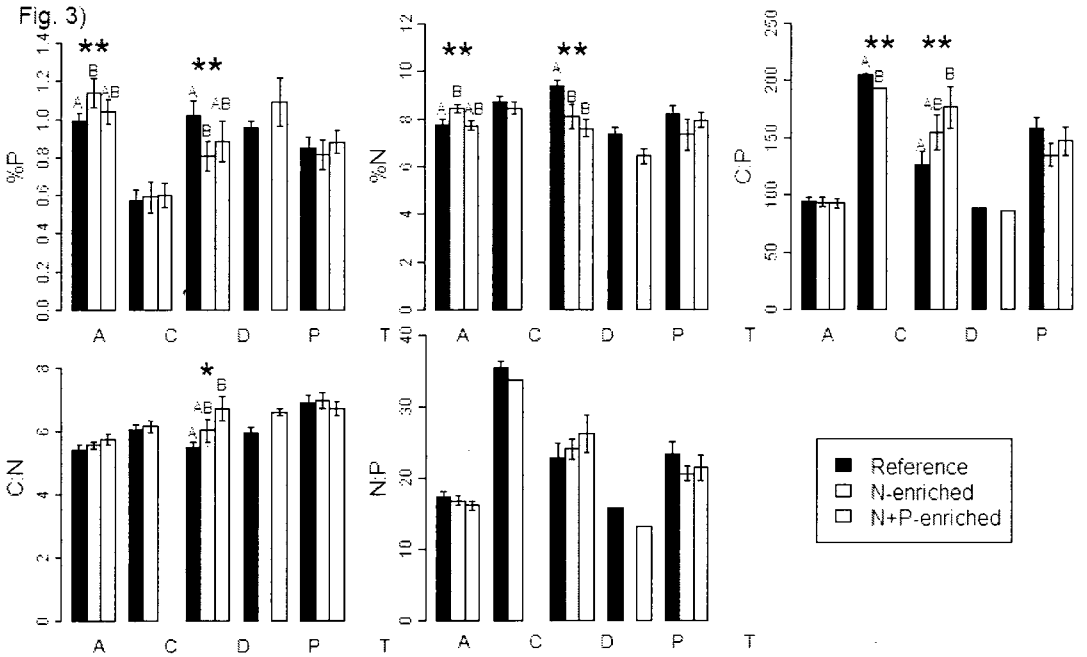


**Figure 3.** Mean nutrient content and ratios of stream benthic macroinvertebrate orders. The different letters along the *x*-axis represent the major orders sampled in the study streams: A=Amphipoda, C=Coleoptera, D=Diptera, P=Plecoptera, and T=Trichoptera. Error bars represent ±1 SE. Different letters above the SE bars indicate significant differences between samples from the stream groups: **=$P<0.05$, *=$P<0.1$.

The nutrient content of most macroinvertebrate taxa was unaffected by higher nutrient loads in suburban streams. Homeostasis was maintained in most taxa. Nevertheless, some taxa did exhibit a deviation from strict homeostasis (Fig. 5). Of the taxa that had different body stoichiometry among stream groups, no clear pattern emerged in which urban or REF streams had consistently higher N or P content. There were significant differences in %P and %N among the stream groups for *Gammarus*, leeches, and Tipulidae. The trichopteran *Ceraclea* spp. and Chironomidae had measurable differences in %N. *Gammarus* and leeches collected in the high-N streams had higher %P than *Gammarus* and leeches in the N+P and REF streams, while Tipulidae from the REF streams had higher %P than those in the N or N+P streams. The leeches from the high-N and high-P streams had significantly lower %P content than those from

the other streams. *Ceraclea* spp. had lowest %N in the REF streams, Tipulidae and Chironomidae had higher %N in the REF streams, and *Gammarus* and leeches had higher %N in the high-N streams. The elmid *Macronychus glabratus* and trichopteran *Goera calcaratta* consistently had very low %P in all the stream groups, while the nemourid stonefly *Shipsa rotunda* consistently had the lowest %N over all the stream groups.

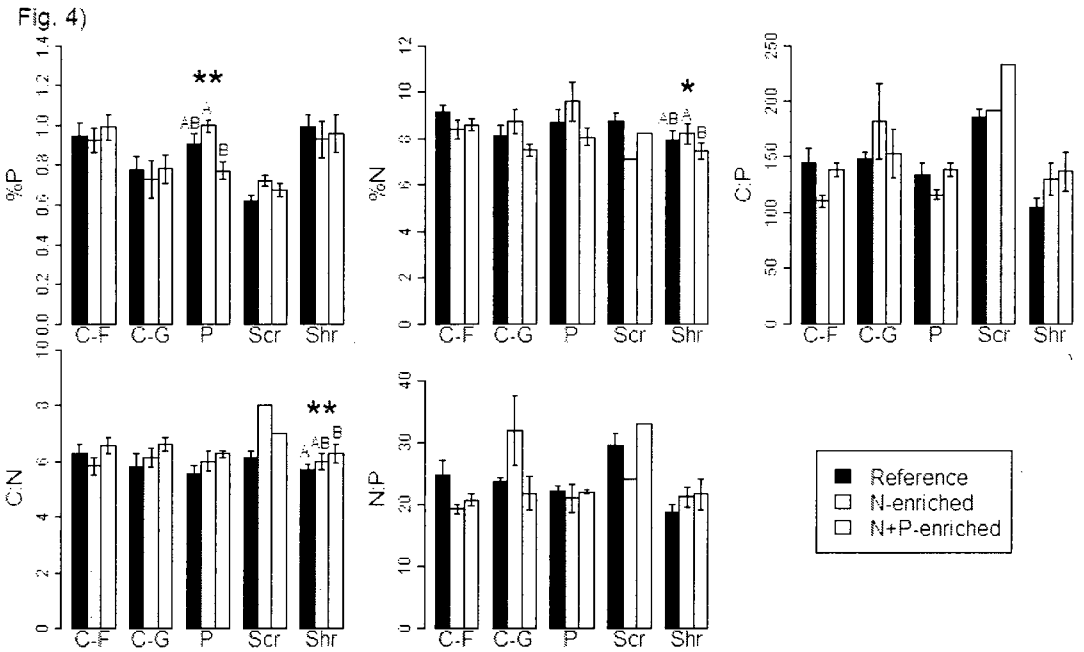


**Figure 4.** Mean nutrient content and ratios of functional feeding groups. The designations along the *x*-axis represent the FFGs: C-F=collector-filterers, C-G=collector-gatherers, P=predators, Scr=scrapers, Shr=shredders. Error bars represent ±1 SE. Different letters above the SE bars indicate significant differences between samples from the stream groups: **=$P<0.05$, *=$P<0.1$.

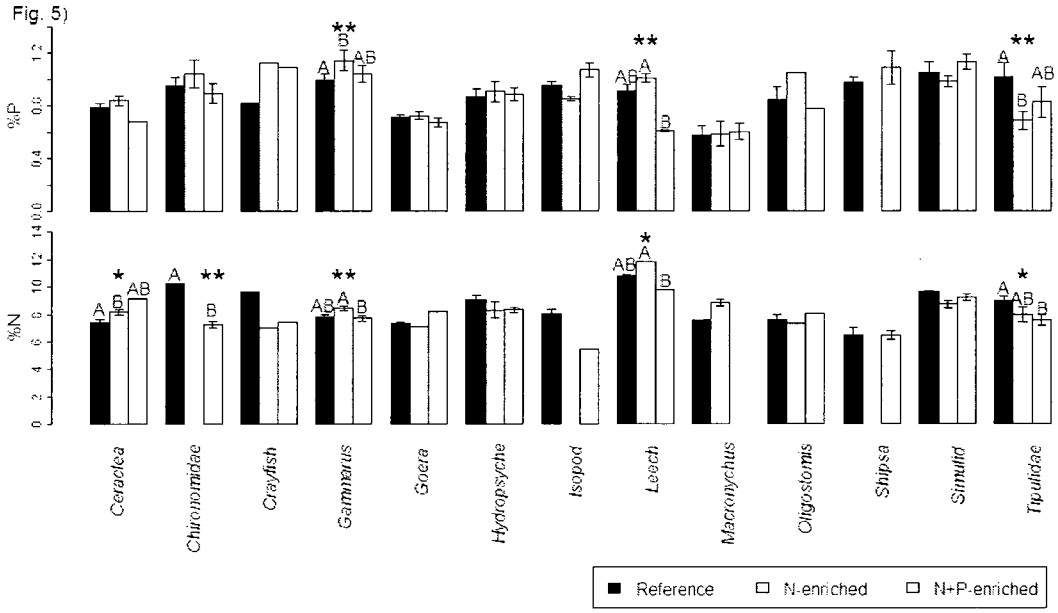


**Figure 5.** Mean nutrient content and ratios of taxa present in all stream groups. Error bars represent ±1 SE. Different letters above the SE bars indicate significant differences between samples from the stream groups: **=$P$<0.05, *=$P$<0.1.

## Nutrient Imbalances

Despite the influence of non-point source pollution on basal food resources, few statistical differences among stream groups were observed for nutrient imbalances between food sources and consumers (Fig. 6). In cases in which statistical differences did occur, the REF streams did not always have higher imbalances than the urban streams as originally hypothesized. The P-content imbalance between collector-filterers and SPOM was significantly higher in the N+P streams (0.76%) than in the REF streams (0.45%; $P$=0.03). The shredders had the highest P imbalance relative to their food source, while all other FFGs, except predators, had N imbalances similar to one another. Predators had the lowest overall imbalances for both %N and %P in all streams. The %N and %P imbalances for predators in the N- and P-enriched streams were both negative, suggesting surplus N and P was being excreted by predators in these streams. No

significant relationships were observed between body length and any nutrient content data.

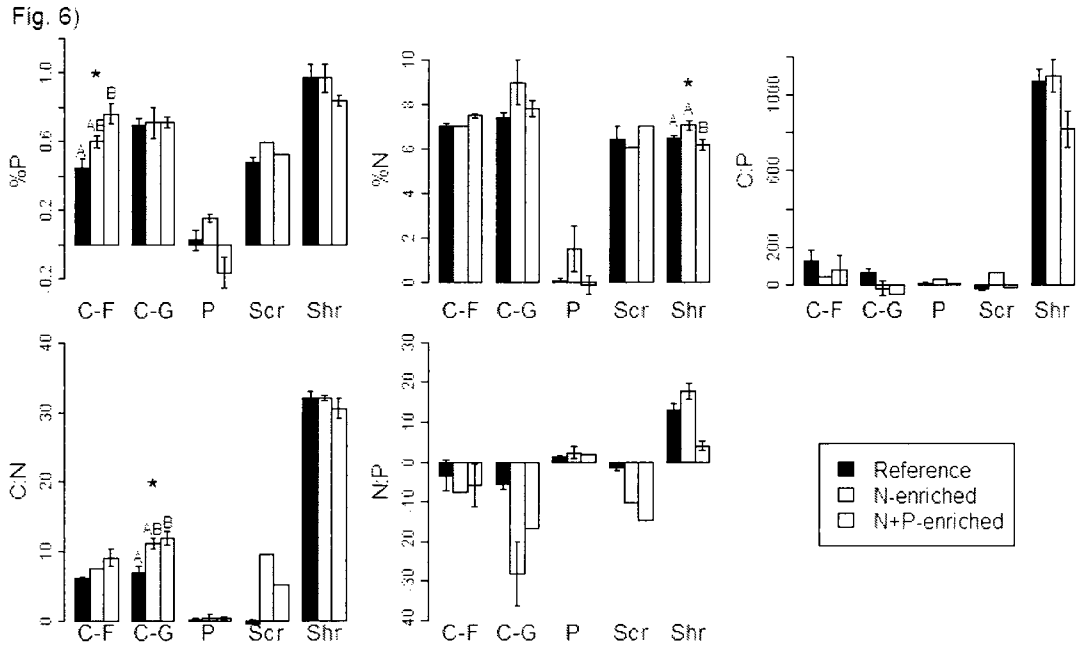


**Figure 6.** Mean nutrient imbalances between FFG and respective food resources. The designations along the *x*-axis represent the nutrient imbalance between FFGs and respective food resource: C-F=collector-filterers -- SPOM, C-G=collector-gatherers -- FBOM, P=predators – primary consumers, Scr=scrapers -- epilithon, Shr=shredders – leaf litter. Nutrient imbalances were calculated by subtracting the mean value for the consumer from the mean value for the food resource. Error bars represent ±1 SE. Different letters above the SE bars indicate significant differences between samples from the stream groups: **=$P<0.05$, *=$P<0.1$.

# CHAPTER III: DISCUSSION

This study was designed to assess how higher nutrient loads caused by non-point source pollution in suburban watersheds affect the different components of stream food webs. Our focus was nutrient enrichment, so our study was not designed to test the numerous other impacts associated with the urban stream syndrome (e.g. flashier hydrology, higher pesticide loading, etc.). Furthermore, specific focus was given to how individual changes to the food web might influence nutrient cycling within suburbanized streams.

## Elemental variation in basal food resources

Contrary to our original hypothesis, higher nutrient loads in suburban streams did not cause a concurrent increase in nutrient content of basal food resources. However, suburban nutrient loads did shift the stoichiometric quality of some basal food resources by lowering their N:P ratio. Furthermore, these shifts were not uniform and the most abundant food resource (leaf litter) was the least affected. One factor that could explain why algal N:P declined with increased nutrient loading is that there was a change in epilithon type and species. Periphyton species and community structure have been shown to be more responsive to artificial nutrient enrichment than periphyton biomass (Stelzer and Lamberti, 2001). Higher nutrient loads likely affected the primary producer communities at our suburban sites, in conjunction with uncontrolled additional factors such as pollutants, road salt, temperature and hydrology that are associated with the urban stream syndrome (Walsh *et al.*, 2005). One of our more puzzling results, that epilithon

%N declined in high-N streams, is perhaps best explained as a secondary result of likely changes in epilithon species composition. Although we did not identify changes in epilithon species in this study, previous studies of nutrient-enriched streams show that changes in algal composition can drive changes in nutrient content and nutrient ratios of epilithon (Bowman *et al.*, 2005, Slavik *et al.*, 2004).

The negative linear relationships between basal food resource N:P and in-stream $PO_4$ concentrations is evidence of increased direct uptake of $PO_4$ from the water column in urban streams. In urban streams with higher dissolved phosphorus concentrations, this direct P uptake would lower basal resource N:P. Potential mechanisms behind the negative relationship between TDN and basal resource N:P were not as apparent. Although one potential explanation would be that the relationship was still driven by increasing $PO_4$ (e.g. that increases in TDN concentration are lower in magnitude than those of $PO_4$), there was no linear relationship between TDN and $PO_4$ concentrations. The negative relationship between TDN and basal resource N:P could represent a decoupling of in-stream TDN with both epilithon and FBOM in suburban streams. TDN is present in such excess that minor changes in TDN concentration do not affect epilithon and FBOM stoichiometry; those changes may therefore have been driven by other factors. Stream periphyton stoichiometry can vary widely and is influenced by a number of environmental conditions, such as hydrology, light, temperature (Godwin, Arthur and Carrick, 2009). Johnson, Tank and Dodds (2009) concluded that human land-use typically decreases the degree of nutrient limitation for both heterotrophic and autotrophic biofilms. Higher nutrient inputs into the suburban streams, in conjunction with the other environmental impacts of suburban watersheds (e.g. flashier hydrology,

temperature fluctuations, chemical impacts, etc.) could be affecting N uptake differently than P uptake.

Expected responses of in-stream leaf litter stoichiometry to suburban nutrient enrichment may have been outweighed by other physical, chemical and biological impacts of suburbanization in the watershed. Due to their heavily forested riparian zone, the streams in this study are expected to be net heterotrophic, with leaf litter as the dominant source of carbon. Dodds (2007) argued that in systems with a ready supply of external carbon (e.g. leaf litter), adding inorganic nutrients generally stimulates production. Furthermore, Mulholland et al. (1985) found that coarse particulate organic matter (CPOM) in a forested stream in Tennessee had the greatest uptake of P during experimental P additions. Recent research suggests that the effects of nutrient enrichment are greatest immediately after leaves enter the stream, with lower magnitude changes after longer periods in the stream (Webster *et al.*, 2009). Both higher production and greater P uptake would be expected to increase the nutrient content of leaf litter in streams affected by suburbanization. The leaf litter samples in this study did not provide evidence of this response, neither in the in-situ samples nor in the standardized litter bags. We suspect that the impacts of suburbanization in the watershed, specifically flashy hydrology and/or higher physical breakdown of organic matter (Walsh *et al.*, 2005, Meyer *et al.*, 2005, Paul and Meyer, 2001), masked these processes in our study streams. Overall, different basal food resources in suburban streams did not show a consistent response to nutrient enrichment, and other factors associated with the urban stream syndrome may differentially affect processes observed in other studies.

## Impacts of suburbanization on macroinvertebrate homeostasis

Although the nutrient content of most macroinvertebrate taxa was not affected by nutrient enrichment, some taxa did exhibit deviation from strict homeostasis. Our hypothesis that P content would vary in consumers was rejected. Of the taxa that did not exhibit homeostasis, most showed differences in body N content, while samples from N- and P-enriched suburban streams did not have uniformly higher P content, suggesting that shifts in body P content were not the only mechanism altering body stoichiometry.

In our study, order, FFG and taxon had greater influences on body stoichiometry than did stream group, suggesting that impacts to a stream that alter community composition and food web structure are more likely to influence the stoichiometry of the food web than simple increases in nutrient concentrations. However, unlike many experimental stream fertilizations that only last a short time, these stream ecosystems have presumably equilibrated to their suburban nutrient loads, and it is possible that the observed changes to community structure were ultimately driven by nutrient concentrations. Instances where higher nutrient inputs are the sole impact to a stream are rare in the absence of a point source discharge, however. Agricultural and urban watersheds are the source of most non-point source pollution (Carpenter *et al.*, 1998). As a result, most streams with higher nutrient loads will also experience additional impacts from urban (Paul and Meyer, 2001, Walsh *et al.*, 2005) or agricultural (Blann *et al.*, 2009) land-use. Therefore, it is vital to understand how macroinvertebrates respond to the interaction of nutrient enrichment with additional, potentially confounding factors in urban and agricultural streams.

P content among all macroinvertebrates was more variable than C or N content, suggesting that macroinvertebrate P content is more responsive to environmental changes than C or N content. Previous studies have reported similar patterns for coefficients of variation, with CV values for P similar to those in this study (CV=52%, Cross *et al.*, 2003; CV=20%, Evans-White and Lamberti, 2005).

Crustacean populations in the headwater streams of this study influenced patterns of overall macroinvertebrate stoichiometry. Amphipods (*Gammarus* spp.), the dominant crustacean, had higher P content, lower N:P and C:P, and similar N content to other invertebrate orders. This pattern has been previously observed in other crustacean taxa and has been attributed to higher rRNA content and P associated with elevated calcium levels (Vrede, Andersen and Hessen, 1999, Evans-White and Lamberti, 2005). However, in one study of Midwest U.S. streams, there was no evidence that watershed or in-stream impacts affected the elemental composition of crustaceans (Evans-White and Lamberti, 2005). In this study, *Gammarus* spp. sampled from high-N streams had higher N and P content compared to those from the REF streams. Furthermore, *Gammarus* spp. are tolerant to nutrient enrichment and high salinity typical of suburban runoff in New England, and this taxon is often found in high abundance in suburban, headwater streams (Meidel, 2005).

Feeding strategy (i.e. FFG) affected macroinvertebrate stoichiometry in this study more than increased nutrient loads from suburbanization. However, nutrient regime did influence variation within FFG. Previous studies have observed higher %N in predators than in primary consumers (e.g. Fagan *et al.*, 2002, Cross *et al.*, 2003, Evans-White and Lamberti, 2005, but see Bowman *et al.*, 2005). This study yielded mixed results across

the different stream groups, with the %N of predators being highest of all FFGs in the N-enriched streams, but similar to other FFGs in REF and N+P streams. Predator %N did not change across stream groups. P content in this study was lowest for scrapers, with among-stream variability for FFGs less than between-FFG variability, which was also observed by Cross *et al.* (2003). Stream group was significant for the stoichiometry of some FFGs (predator %P, shredder %N, shredder C:N), but these changes were not consistent. While some FFGs exhibited significant changes in elemental content among stream groups, most FFGs exhibited homeostasis in response to suburban nutrient enrichment.

Suburban nutrient enrichment did not affect the body stoichiometry of most macroinvertebrate taxa, and those species that did respond to nutrient enrichment responded differently than hypothesized. We predicted that there would only be significant differences in P content. However, more taxa had significant differences in N content than P content (5 vs. 3) among stream groups. Among all taxa that responded to suburban nutrient enrichment, there was no clear pattern for either %N or %P. Some taxa had higher nutrient content in REF streams than in N or N+P suburban streams, while others showed the opposite response. A response to increased stream P loads by allocating more P to rRNA, (i.e. the growth rate hypothesis; (Schade *et al.*, 2003) might explain higher %P in N+P streams. Alternatively, higher P content of taxa in N streams could be a response to periodic high P, whereby organisms store P in haemolymph or insect tissue (Woods *et al.*, 2002). While changes in P content have been observed in previous studies (e.g. DeMott, Gulati and Siewertsen, 1998, Cross *et al.*, 2003, Evans-White and Lamberti, 2005, Shimizu and Urabe, 2008), this is the first study to measure

differences in N content among consumers that appear to be associated with shifts in dissolved nutrient inputs.

## Effects of non-point source pollution on nutrient imbalances in headwater streams

Although no statistical difference in nutrient imbalances among stream groups was observed in this study, changes in basal food resource stoichiometry could potentially affect food web dynamics in suburban streams. When considering nutrient imbalances, two caveats must be considered. First, FFG is determined by mode of feeding, not by direct analysis of food sources (e.g. gut content analysis; Merritt and Cummins, 1996). Secondly, macroinvertebrates might selectively feed on higher quality components of the bulk resource, such as the fungal species that colonize leaf litter (e.g. Arsuffi and Suberkropp, 1985). The imbalances presented in this paper are estimated from bulk samples. If a macroinvertebrate selectively feeds or eats something different than predicted based on their FFG classification, the actual nutrient imbalance would be different than the estimated imbalance. Therefore, while we found no statistical difference between nutrient imbalances in suburban or reference streams, there could be a substantial difference in the imbalance for individual consumers due to the changing stoichiometry of their basal food resources.

Nutrient imbalances were bounded by predators with the lowest imbalances and shredders with the highest imbalances, consistent with other studies (e.g. Cross *et al.*, 2003). Predators consume food with a relatively high nutrient content, leading to lower imbalances, as determined from %N, %P, and nutrient ratios. Additionally, predators

were the only FFG for which we measured the stoichiometry of what was actually ingested (i.e. other invertebrates). Of the primary consumers, the shredders' food resource (leaf litter) has the lowest overall quality. The extremely high imbalances for C:N (~3-6× higher) and C:P (~10× higher) were driven by the high %C of leaf litter. Values in both the suburban and reference streams were lower than those found by Cross *et al.* (2003) in an enriched and a reference stream in North Carolina.

## Potential impacts of suburbanization on nutrient dynamics

Suburban non-point source pollution in headwater streams affects the stoichiometry of basal food resources more than that of consumers, which could shorten gross nutrient uptake lengths and increase nutrient recycling rates by consumers in suburban streams. The extent of this influence, however, would be influenced by any changes in biomass of basal resources and macroinvertebrate consumers, as well as the imbalance between consumers and the basal resource that provides the most energy to consumers (in this case, detritus).

Stoichiometric changes to basal food resources in suburban streams can increase nutrient demand relative to ecosystems with basal food resources that do not respond to in-stream nutrient concentrations through altered food web stoichiometry. Increasing the nutrient content of basal food resources will increase nutrient uptake rates ($V_f$) and shorten uptake lengths ($S_w$) for dissolved N and P (Cross *et al.*, 2005). These changes to nutrient spiraling will depend on the magnitude of change to benthic stoichiometry and biomass, with a stream that has high biomass and substantial changes in stoichiometry resulting in a greater influence on nutrient spiraling parameters. Furthermore, changing

the stoichiometry of basal food resources will potentially increase overall nutrient transfer to higher trophic levels via higher invertebrate production (Cross, Wallace and Rosemond, 2007). Suburban systems often have additional impacts that influence basal food resource biomass and composition, such as riparian deforestation that increases epilithon biomass and decreases in leaf litter detritus. These biomass changes, in concert with stoichiometric changes, can lead to substantial changes in stream nutrient spiraling, with net increases or decreases in nutrient storage by the ecosystem.

Suburban impacts on the macroinvertebrate population composition can affect in-stream nutrient cycles. Nutrient recycling in stream systems can be affected by changes in consumer biomass, N:P ratio and degree of homeostatic regulation (Small *et al.*, 2009). Suburbanization has previously been shown to decrease overall macroinvertebrate abundance (i.e. Meidel, 2005). However, within any overall decrease, some taxa (e.g. Chironomidae, oligochaetes, amphipods) actually increase in abundance in urban and suburban streams (Paul and Meyer, 2001, Meidel, 2005, Walsh *et al.*, 2005). This study shows that a small subset of taxa found in suburban streams exhibit a stoichiometric response to suburban nutrient enrichment. An overall biomass decline would be expected to minimize the impacts of consumer-driven nutrient recycling, manifesting as higher downstream flux of N and P (Small *et al.*, 2009). However, if there is any increase in the biomass of taxa storing the limiting nutrient (for example, non-homeostatic taxa with luxury P-uptake) within an overall biomass decline, then the changes to nutrient recycling might actually be reversed, resulting in a decrease in downstream nutrient velocity. Therefore, understanding the specific biomass changes for both the homeostatic and non-homeostatic consumers could be more important than overall consumer biomass changes.

# CHAPTER IV: CONCLUSION

Few studies have looked at the impacts of suburbanization on stream food webs. Our results confirm that some stream benthic macroinvertebrates do not exhibit strict homeostasis, and that their stoichiometry can be affected by nutrient loads typical of many suburban watersheds. Overall this variation in body stoichiometry is less than the differences between different taxonomic classifications or FFGs, as well as being less than the change in elemental content of their food resources. However, the changes we observed did not follow a general pattern and could not be attributed to simple mechanisms such as luxury storage of P. While the stoichiometry of some taxa supports high body P content, other taxa showed a decrease with higher stream P loads. Further research to determine specific mechanisms for these changes is necessary to better understand the implications for consumer-driven nutrient recycling in suburban streams.

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